

# Morphological differentiation and speciation among darters (*Anhinga*)

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**SUMMARY.**—Morphological analysis of the major populations of Old World darters (*Anhinga* spp.) from Africa to Australia identified significant regional differentiation in sexual dimorphism, shape and structure of the pale cheek stripe, pattern and tone of the chin and foreneck, form of scapular feathering, and marking and tone of the greater wing-coverts. Further differentiation was found in the proportions of tail, bill and feet, and in bare-part colours, particularly in the irides and feet. Among the three major forms—Afro-Middle East *rufa*, Oriental *melanogaster* and Australasian *novaehollandiae*—qualitative differentiation in plumage patterning was almost of the same high order as that between these darters and the Anhinga *A. anhinga* of the New World. Furthermore, differentiation of a lower but still clear-cut order was found among African, Malagasy and Middle East populations of *rufa*, and between Australian and New Guinean populations of *novaehollandiae*. We conclude that *rufa*, *melanogaster* and *novaehollandiae* have speciated, and that Malagasy, Middle East and New Guinean isolates are subspecies of African *rufa* and Australian *novaehollandiae* respectively.

It is conventional today to recognise two species of *Anhinga*: the Anhinga *A. anhinga* in tropical and subtropical America and the Darter *A. melanogaster* from Africa across southern Asia to Australasia in the Old World (Voous 1973, Wolters 1975, Cramp & Simmons 1977, Dorst & Mougín 1979, Brown *et al.* 1982, M. D. Bruce in White & Bruce 1986, Marchant & Higgins 1990, Orta 1992, Johnsgard 1993, Inskipp *et al.* 1996, Wells 1999, Dickinson 2003). Yet while the status of the American anhinga has hardly been in question, the populations of Old World darters have been in a state of taxonomic flux throughout the later 20th century. Peters (1931), first to employ the polytypic species concept in a global list of birds, treated them as three species: Afro-Middle East *rufa* Daudin, 1802, Oriental *melanogaster* Pennant, 1769, and Australian *novaehollandiae* Gould, 1847. In *rufa*, furthermore, he distinguished three subspecies: nominate *rufa* through sub-Saharan Africa, *vulsini* Bangs, 1918, in Madagascar and *chantrei* Oustalet, 1882, in the Middle East. Vaurie (1965) and Mayr & Short (1970) accepted Peters' species, the former concluding that morphological differentiation among *rufa*, *melanogaster* and *novaehollandiae* was too great for any lumping.

Since then, nevertheless, there has been a cascade of lumping, sparked by Voous (1973), Wolters (1975) and Condon (1975) placing all Old World forms in one species. They were promptly supported by Harrison (1978) with his finding of common structure and tendinal canals in tarsometatarsi, although his sample was small and possibly affected by age. Except the AOU (1983), Sibley & Monroe (1990), Andrew (1992), Rasmussen & Anderton (2005) and Kirwan *et al.* (2008) who maintained the three species of Peters (1931), other major revisers followed the lead of Voous, Wolters, Condon and Harrison, and demoted Peters' species to subspecies—see references above. Consequent casualties were most of Peters' (1931) subspecies, and at times even certain of his species names. Condon (1975) and Dorst and Mougín (1979), for example, combined African and Australian darters (*rufa*, *novaehollandiae*) in one subspecies separate from the intervening Oriental darter

(*melanogaster*). Zoogeographically it was absurd, justified by the dubious observation that 'Australian birds were virtually indistinguishable from subspecies *rufa* of Africa' (G. F. van Tets in Condon 1975; H. T. Condon pers. comm.). Most reviewers (including Kirwan *et al.* 2008) also dropped Malagasy and Middle Eastern forms of *rufa*—*vulsini* and *chantrei*—into synonymy, along with subsequently described *papua* Rand, 1938, from New Guinea. Wolters (1975) recognised *chantrei*, and Orta (1992) and Dickinson (2003) listed *vulsini*, but that was all.

Molecular studies have so far added little. MtDNA sequences of African *rufa* and Australian *novaehollandiae* were compared incidentally by Kennedy *et al.* (2005) in a methodological study focused on resolving phylogenetic signal. It showed divergence comparable to levels of mtDNA distance between species of cormorants (*Phalacrocorax*) and boobies (*Sula*). Intervening Oriental *melanogaster* was not included in the study, yet it was enough for Christidis and Boles (2008) to treat all three major Old World forms—*rufa*, *melanogaster* and *novaehollandiae*—as separate species. Apart from the work of Harrison (1978), which is limited in any case, none of the above reviews is supported by an analysis of characters across taxa—morphological or molecular. There have, in fact, been no decent comparative descriptions of how the major continental forms of Old World darters differ from one another since Ogilvie-Grant's (1898) account over 100 years ago. Towards filling this gap and providing an explicit rationale for species-group taxonomy in the Old World darters, we offer here a detailed morphological analysis of all regional forms, together with conclusions concerning taxonomic status.

## Materials and Methods

This study is based on dry skin material of all Old World populations of darters preserved in the globally rich and comprehensive collections of the American Museum of Natural History, New York (AMNH), augmented by series' in Australian national and provincial museums: Australian Museum, Sydney (AM); Australian National Wildlife Collection, Canberra (ANWC); Museum Victoria, Melbourne (MV); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAMA); and Western Australian Museum, Perth (WAM). We also examined the small collections of New Guinean material in the Papua New Guinea National Museum, Port Moresby (PNGNM). These series were compared among themselves and with a selection of 15 males and 15 females of nominate *A. anhinga* in AMNH, as an out-group. Altogether 275 adult specimens of both sexes were compared. The numbers of each sex of each taxon examined are given in the header to Table 1, and the numbers of selected specimens measured are given against taxon and sex in Table 3.

We analysed plumage patterning from long series laid out by region. As well as taking standard measurements (wing, tail, bill and tarsus) to assess gross size, moreover, we also calculated ratios to compare allometric proportions, which are usually more significant indicators of adaptation and differentiation. Wing was measured as flattened chord, tail as the length of the central rectrices, bill from the tip to feathers on culmen, and tarsus from the notch on the heel to the top of the knuckle bridging the base of the toes. Bare-part colours, recorded inconsistently in museum collections, were augmented and teased out for age and sex from details in handbooks (Palmer 1962, Cramp & Simmons 1977, Brown *et al.* 1982, Marchant & Higgins 1990) and photographs (Orta 1992; internet, only for taxa identifiable by plumage).

## Morphological analysis

*Qualitative differentiation in plumage patterns.*—The results of plumage analysis are detailed in Table 1. They show a pattern of regional differentiation in principally three sets of characters: (1) face and throat pattern, (2) upperwing pattern and (3) gross ventral pattern. Differing from plain-headed American *anhinga*, all Old World populations share a pale cheek-side neck stripe in both sexes in both breeding and non-breeding plumages. But there the similarity among them ends. In *rufa*, *vulsini* and *chantrei*, the stripe is moderately long and slender, in *melanogaster* still longer and narrower, but in *novaehollandiae* and *papua* short and broad. Furthermore, the structure of its feathering differs. In *melanogaster* and the Australasian group, its penna resemble feathering elsewhere on the face and neck in all seasons, but in *rufa*, *vulsini* and *chantrei*, they become distinctively if shortly plumose during breeding (Cramp & Simmons 1977) and terminate in short rust-brown hairs as they wear. Such pluming may be homologous with the longer white, rufous and black plumes that develop on the sides and back of the head and neck in breeding male and female *anhinga*. On the throat, breeding males of all regional forms differ as detailed in Table 1, with primary differentiation between *rufa* / *vulsini* (rufous with ill-defined white border to chin), *melanogaster* (spotted blackish on white), *novaehollandiae* / *papua* (black with clear broad white border) and *anhinga* (plain black). The creamy throat of male *chantrei* may reflect more the retention of non-breeding foreneck tone than any substantive difference in pattern from the *rufa* group.

In upperwing pattern, *anhinga* again stands out in the brilliance of its broad silver-grey sash across the shoulders (wing-coverts). The effect of this grey sash, centred on the greater wing-coverts, is enhanced by a lack of black bordering to the feathers there. It produces a contrasting three-band wing pattern: a distal all-black remige band and a proximal inner covert band of black spotted silver, split by a broad plain silver median band through the greater coverts. This sash is present in all Old World regional groups, but is never as broad and bright as in *anhinga*, and its feathering is bordered with black on the greater as well as the inner coverts (Table 1). In *novaehollandiae* and *papua* it is still distinct, and indeed paler, broader and rather *anhinga*-like in females, but because of black feather edging and darker toning, the greater wing-coverts in males blend with the inner and together contrast with the all-black remiges in more of a two-band pattern. There is no sexual dimorphism in *melanogaster*, but the grey tone to the feather centres is as silvery as in female *novaehollandiae* / *papua* or even whiter, producing a more contrasting two-band pattern against the all-black body of both sexes. In both sexes of *rufa*, and to a lesser extent of *vulsini* and *chantrei*, the pale greater wing-coverts band is narrowest and dullest of all, even fuscous in tone. It neither stands out as a discrete band as in *anhinga* and female *novaehollandiae* / *papua*, nor blends with the inner coverts to contrast with the remiges as in *melanogaster* and male *novaehollandiae* / *papua*. Rather, it has the appearance of a dull narrow divider between the inner coverts and remiges in an almost monotone wing pattern. Differences in the upperwings extend to the scapulars which are very long and attenuate with dull buffy-grey shafts in *rufa* and *vulsini*, similar in form but with silvery shafts in *chantrei* and *melanogaster*, rather short, abruptly acute and dull grey-shafted in Australasian *novaehollandiae* and *papua*, and of intermediate form and silvery shafted in *anhinga*.

Seasonal cycles, sexual dimorphism and ontogeny complicate the expression of gross ventral pattern. It is simplest in adults of the Afro-Oriental forms, in which non-breeding plumage resembles breeding, and females resemble males except for paler and duller toning respectively (Cramp & Simmons 1977). In these populations, black over the lower ventral region extends to the top of the lower foreneck, where it is abruptly demarcated from



TABLE 1  
 Traits of adult breeding plumage in Old World regional forms of *Anhinga*, and of American *A. anhinga*.  
 Most but not all adults in the sample sizes quoted for each form are in breeding plumage.

Trait	<i>rufa</i> n=24♂♂, 20♀♀	<i>vulsiini</i> n=4♂♂, 5♀♀	<i>chantrei</i> n=8♂♂, 10♀♀	<i>melanogaster</i> n=21♂♂, 12♀♀	<i>papua</i> n=4♂♂, 12♀♀	<i>novaeollandiae</i> n=62♂♂, 63♀♀	<i>anhinga</i> n=15♂♂, 15♀♀
Range	sub-Saharan Africa	Madagascar	Middle East	Pakistan to SE Asia, Greater Sundas and Sulawesi	New Guinea	Australia	tropical / subtropical Americas
White line edging frons to behind eye	faint to absent	faint to absent	faint to absent	consistently present	mostly absent to faint	mostly absent to faint	absent
Male upper head and hindneck	blackish	dusky brown	brownish to cream-brown on hindneck	brown speckled dusky, straw and fawn	black	black	black
Pale cheek stripe	dagger-shaped, length ½ neck c.5-7 mm wide	dagger-shaped, length ½ neck c.5-7 mm wide	dagger-shaped, length ½ neck c.5-7 mm wide	stiletto-shaped, length ½ neck c.3-5 mm wide	lanceolate, length ¼ neck, 10-15 mm wide	lanceolate, length ¼ neck, 10-15 mm wide	absent
Cheek stripe pluming	shortly hairy-plumose	shortly hairy-plumose	shortly hairy-plumose	shortly non-plumose	shortly non-plumose	shortly non-plumose	-
Head-sides pluming	absent	absent	absent	absent	absent	absent	present
Male throat pattern	plain rufous with faint white rim to gular pouch	plain rufous with faint white rim to gular pouch	plain creamy white to rusty cream	extensively white, finely spotted black	plain black with broad white rim to gular pouch	plain black with broad white rim to gular pouch	plain black
Male foreneck pattern	plain rich rufous, paler non-breeding	plain rich rufous, paler non-breeding	plain creamy white to rusty cream	mid brown, speckled dusky	plain black with variable patch of chestnut in centre	plain black with variable patch of chestnut in centre	plain black
Form of scapular feathering	attenuately elongate	attenuately elongate	attenuately elongate	attenuately elongate	shortly acute	shortly acute	medium short and acute

Trait	<i>rufa</i> n=24♂♂, 20♀♀	<i>vulsini</i> n=4♂♂, 5♀♀	<i>chantrei</i> n=8♂♂, 10♀♀	<i>melanogaster</i> n=21♂♂, 12♀♀	<i>papua</i> n=4♂♂, 12♀♀	<i>novaeollandiae</i> n=62♂♂, 63♀♀	<i>anhinga</i> n=15♂♂, 15♀♀
Form of pale scapular marking	fine shaft spot-streaks over most of mantle	fine shaft spot-streaks over most of mantle	fine shaft spot-streaks over most of mantle	fine shaft-spots over most of mantle	narrow shaft- streaks confined to scapulars	narrow shaft-streaks confined to scapulars	fine shaft-spots over all of mantle
Colour of pale dorsal shaft-marks	dull dirty grey to buffy grey	dull dirty grey to buffy grey	whitish grey	bright whitish grey	dull pale grey to buffy grey, greyer in ♀♀	dull pale grey to buffy grey, greyer in ♀♀	whitish grey
Black edging to greater wing-coverts	present and narrow both sexes	present and narrow both sexes	present and narrow both sexes	present and broad both sexes	present, reduced in ♀♀	present, reduced in ♀♀	absent
Tone and width of greater wing-covert sash	♂♂ dusky copper, ♀♀ dusky grey, both c.9-12 mm wide	dull dirty pale grey, 10-15 mm wide both sexes	mid grey with fuscous wash, 10-15 mm wide both sexes	bright whitish grey, 10-15 mm wide both sexes	♂♂ dull pale grey, 10-15 mm wide, ♀♀ brighter to 20 mm wide	♂♂ dull pale grey, 10-15 mm wide, ♀♀ brighter to 20 mm wide	bright pale grey, 30-50 mm wide both sexes
Sexual dimorphism	slight dorsally and ventrally	slight dorsally and ventrally	slight dorsally and ventrally	slight dorsally and ventrally	moderate dorsally, marked ventrally	moderate dorsally, marked ventrally	moderate dorsally, marked ventrally
Female face and foreneck	as ♂♂ but duller; neck dull rufous	as ♂♂ but duller; neck dull rufous	as ♂♂ but duller; neck whitish	as ♂♂ but duller	all whitish	all whitish	all russet-tan
Female breast and belly tone	black (as ♂♂)	black (as ♂♂)	black (as ♂♂)	black (as ♂♂)	white	white	black (as ♂♂)
Female dorsum base tone	black grading rufous-brown over hindneck	black grading rufous-brown over hindneck	black grading rufous-brown over hindneck	black grading dull deep brown over hindneck	uniformly dusky grey	uniformly mid brownish grey	black grading rufous-brown over hindneck
Pale tail tip	absent	absent	absent	absent	absent	absent	present

variously rufous, brown and cream tones over the rest of the foreneck. American *anhinga*, in contrast, is markedly sexually dimorphic. Adult males are all black in both breeding and non-breeding plumages, whereas females resemble Afro-Asian males and females in pattern and seasonal tones except for a much lower placed demarcation between the tawny-rufous foreneck and black lower underparts across the mid breast. Sexual dimorphism and seasonal variation is perhaps most complex of all in Australasian *novaehollandiae* and *papua*. In this group, adult males are entirely black when breeding, except for a small patch of rich chestnut confined to the mid foreneck. At other seasons, they remain black to the top of the lower neck, indicative of affinity with Afro-Oriental forms, but become pale to dull deep rufous over the entire mid and upper foreneck. Adult females, by contrast, are entirely greyish dorsally and whitish ventrally, and differ only with season by developing clear black margins to the cheek stripe when breeding. Marchant & Higgins (1990) did not recognise breeding and non-breeding plumages in *novaehollandiae*, but they are identified here from correlating three-year-old birds or older (fully crimped central rectrices and scapulars) with their gonad condition in material in ANWC.

American anhingas have been thought to differ from all Old World forms in their narrowly whitish-tipped tails (Ogilvie-Grant 1898). It is noteworthy then that juveniles of *A. rufa* have been described (Cramp & Simmons 1977) and figured (Cramp & Simmons 1977, pl. 26, Brown *et al.* 1982, pl. 8) with pale tips to the tail. Juveniles of Australian ( $n = 10$ ) and New Guinean ( $n = 3$ ) populations lack this bar (Marchant & Higgins 1990: 827). Thus a pale terminal tail bar is evidently present in juveniles of some Old World populations, but not others, and is lost in all with age. Such changes occur throughout the plumages of the genus. Juveniles of all Old and New World forms are uniformly pale whitish ventrally and dull grey dorsally, and appear to gain adult and sexual plumages progressively into their late second and third years (Palmer 1962, Marchant & Higgins 1990). Different age classes from different regions overlap in these traits during development, because of which analyses here are based on adults with fully crimped central rectrices and scapulars, and particularly those in breeding plumage.

*Variation in bare-part colours.*—Data for bare-part colours in adults of all regional populations (Table 2) reveal significant inter-taxon differentiation in colour of the irides, gular skin and feet, and minor differences in colour of bill and face. Some but not all differentiation is linked with breeding and sex. In the irides, colour is consistently yellow in *melanogaster*, *novaehollandiae* and *papua*, and deep red in *anhinga* at all times, whereas it apparently varies from yellow to red in Afro-Middle East forms (Cramp & Simmons 1977). Bill colour varies little with age, sex and season among regional forms, although it is richest in breeding adults and darker over the maxilla in males, particularly in breeding *anhinga*, enhancing the yellow of the mandible in an otherwise blackish head. Face skin tone is a dull pale yellowish in non-breeders of all taxa except *anhinga* but deepens and brightens in Old World populations during breeding, becoming dark yellow particularly in males. In *anhinga*, the face of non-breeders is variously dull grey, but becomes rich emerald to turquoise in breeding males, less so in females. Gular skin, basically yellow, also varies, becoming blackish in the centre and base in breeding *anhinga* and breeding Afro-Oriental forms, although the tone may be more localised and temporary in the latter. In Australasian populations, however, it appears to remain wholly yellowish at all times. Feet differ among regions as well. In *anhinga* they are prevailing greyish black to black, but in Australasian populations pallid yellowish flesh at all times. Feet colours in Afro-Oriental forms are yellowish, approaching Australasian forms, but are washed consistently greyer and are usually darker. Juveniles of all forms are dull and nondescript in all bare-part colours,

TABLE 2

Soft-parts colours of adult Old World regional forms of *Anhinga* and of American *A. anhinga*. Colours recorded are averaged for easier comprehension. Sexes are separated only where colours between them differ significantly. As a rule, immatures have the colours of non-breeding females and are dull. For sources, see Materials and Methods.

Taxon	Seasonal condition	Iris (both sexes)	Bill (both sexes)	Facial skin	Gular skin (both sexes)	Tarsus/toes (both sexes)
<i>rufa</i> (Sub-Saharan Africa)	breeding	variable: rich yellow to red	rich yellow, maxilla washed horn	dusky yellow (both sexes)	(greenish) black	dusky brown, webs blackish
	non-breeding	as breeding but duller	paler, duller yellow	dull creamy yellow	dull cream in both sexes, sometimes washed black	deep grey-brown to yellowish brown, webs yellower
<i>vulsini</i> (Madagascar)	breeding	yellow (? to red)	rich yellow, maxilla washed horn	dull yellow (both sexes)	blackish	pale grey with yellow wash, webs yellower
	non-breeding	as breeding but duller	paler, duller yellow	as breeding or duller	dull cream	pale greyish yellow, webs yellower
<i>chantrei</i> (Middle East)	breeding	variable: yellow to red	rich yellow, maxilla washed horn	dull yellow (both sexes)	blackish	pale greyish yellow, webs yellower
	non-breeding	as breeding but duller	paler, duller yellow	dull cream	dull cream	pale greyish cream with flesh wash
<i>melanogaster</i> (South-East Asia)	breeding	bright yellow	rich yellow, maxilla washed horn	mid to dark yellow (both sexes)	rich yellow with variable black wash	pale yellow to dark grey, webs yellower
	non-breeding	dull yellow	paler, duller yellow	pale creamy yellow	pale creamy yellow with occasional black wash	pale cream to grey-yellow, webs yellower
<i>novaeollandiae</i> (Australia)	breeding	bright to deep yellow	rich yellow, maxilla washed greenish horn	dark yellow in ♂♂, bright yellow in ♀♀	mid yellow	pale yellowish flesh, webs browner yellow
	non-breeding	dull yellow to pale brown	paler, duller yellow	pale greyish yellow (both sexes)	pale cream	pale greyish flesh, webs yellower
<i>papua</i> (New Guinea)	breeding	as <i>novaeollandiae</i>	as <i>novaeollandiae</i>	as <i>novaeollandiae</i>	as <i>novaeollandiae</i>	as <i>novaeollandiae</i>
	non-breeding	as <i>novaeollandiae</i>	as <i>novaeollandiae</i>	as <i>novaeollandiae</i>	as <i>novaeollandiae</i>	as <i>novaeollandiae</i>
<i>anhinga</i> (New World)	breeding	rich deep red	rich yellow, maxilla washed variably dusky	emerald to blue around eye in ♂♂, duller in ♀♀	black	olive-black
	non-breeding	duller red	dull horn-yellow	dull grey-green in ♂♂, dull yellow-grey in ♀♀	pale greyish yellow	greyish yellow



which are generally of the same tone in non-breeding females. As a rule, the bare parts in breeding males are deeper and more intensely toned than in females.

*Morphometric differentiation in size and proportions.*—Body size, as estimated by wing length (Table 3), differs little among regional Old World forms and nominate American *anhinga*. Furthermore, there is little sexual dimorphism in most forms, particularly the Australasian group. It is most marked in American *anhinga*, in which males are larger than females, and in Malagasy *vulsini*, in which females are larger than males in all parts. Measurements for *vulsini* may be biased by small sample size and the immaturity of two of the four males, although the bills of the latter, always shorter in juveniles, are as long as those of the two adult males. There are, however, regional differences in gross and proportional tail, bill and tarsus length. Both American *anhinga* and Malagasy *vulsini* are longest in tail and bill, and shortest in tarsus, all sexually reversed between the two forms. Sexual dimorphism in proportional bill length is particularly marked in *anhinga*, suggesting partitioning of prey. In contrast, Australasian *novaehollandiae* and *papua* are shortest in tail and bill and longest in tarsi, with virtually no sexual dimorphism. The remaining Afro-Oriental forms, *rufa*, *chantrei* and *melanogaster*, are intermediate in all gross measurements and proportions, with males averaging slightly larger than females.

### Taxonomic synthesis

None of the major regional forms of Old World darters meet, meaning that their interaction cannot be assessed under the Biological Species Concept. Middle Eastern *chantrei* extends east to the lower Tigris-Euphrates wetlands in Iraq and Iran (Khaleghizadeh *et al.* 2011; RP pers. data, including photographs), and Oriental *melanogaster* west to the Indus Valley, but they are separated by almost 2,000 km of unsuitable habitat along the coast and hinterland of Iran and west Pakistan. In the Indonesian archipelagos, *melanogaster* extends east to Sulawesi as a breeder (White & Bruce 1986), while Australasian *novaehollandiae* ranges north-west to Timor-Leste and Roti (Trainor 2005a,b) in the Lesser Sundas, c.600 km south-east of Sulawesi. On Timor-Leste, where Trainor (2005a) found *novaehollandiae* breeding, McKean *et al.* (1975) had earlier recorded nominate *melanogaster*, suggesting sympatry. But as McKean *et al.* (1975) gave no diagnostic details of the darters they saw, identity may have been presumed and the record requires confirmation (White & Bruce 1986). Elsewhere in that region only *novaehollandiae* has been recorded, in both the south Moluccas and Banda Sea islands, invariably as a vagrant from either Australia or New Guinea (White & Bruce 1986). New Guinean (*papua*) and Australian (*novaehollandiae*) populations of the Australasian group may mix to some degree in the Trans-Fly region of southern New Guinea and on the Cape York Peninsula, Queensland. Nevertheless, sampling to date (1♂, 5♀♀ from the Trans-Fly, 6♂♂, 4♀♀ from the Cape York Peninsula) does not show it morphologically (see below). In the absence of confirmed interaction between contiguous populations of any taxa, then, estimates of speciation must rely on levels of morphological, behavioural and molecular differentiation.

The combined morphological data indicate that Old World darters as a group are well differentiated from American *A. anhinga*. All lack breeding plumes on the head-sides and pale-tipped tails when adult, and they share pale cheek stripes, black feather borders to a narrower pale sash across the greater wing-coverts, and feet and facial colours dominated by pale flavonoid pigmentation. Levels of sexual dimorphism in size and proportions are also low. Yet among themselves, Afro-Middle East, Oriental and Australasian groups are almost as deeply differentiated as any one of them is from *anhinga*. The Australasian group is most divergent with a short, broad cheek stripe, black-necked breeding plumage, with a broad white chin fringe in males, short scapulars, uniquely white-ventered females in all



TABLE 3

Measurements of adults and near adults of all regional forms of Old World *Anhinga*, and of American *A. anhinga*; range plus means (in parentheses). For source and selection of samples, see Materials and Methods.

Taxon	Sex	<i>n</i>	Wing (mm)	Tail (mm)	Culmen (mm)	Tarsus (mm)	Tail/wing ratio	Culmen/ wing ratio	Tarsus/wing ratio
<i>rufa</i> (Sub-Saharan Africa)	♂♂	18	336–366 (349.7)	220–260 (236.4)	73.0–85.0 (80.0)	39.0–47.3 (44.8)	0.63–0.75 (0.68)	0.205–0.240 (0.229)	0.121–0.133 (0.126)
	♀♀	10	333–357 (343.6)	230–246 (237.1)	70.3–80.7 (75.9)	41.4–46.3 (43.2)	0.66–0.71 (0.69)	0.210–0.240 (0.221)	0.115–0.135 (0.126)
<i>vulsini</i> (Madagascar)	♂♂	4	335–347 (343.0)	235–258 (249.8)	75.2–85.2 (80.1)	43.1–44.3 (43.9)	0.70–0.74 (0.73)	0.217–0.246 (0.234)	0.124–0.131 (0.128)
	♀♀	5	343–365 (354.2)	261–280 (269.0)	77.0–92.5 (84.6)	40.6–48.2 (44.2)	0.73–0.77 (0.76)	0.220–0.265 (0.237)	0.116–0.137 (0.125)
<i>chantrei</i> (Middle East)	♂♂	7	337–359 (347.1)	228–237 (232.0)	80.2–88.3 (84.7)	44.2–47.0 (45.5)	0.65–0.70 (0.67)	0.233–0.257 (0.244)	0.124–0.137 (0.131)
	♀♀	6	328–344 (336.2)	208–228 (219.5)	76.0–85.9 (81.5)	43.4–49.6 (45.8)	0.63–0.68 (0.65)	0.222–0.255 (0.242)	0.127–0.144 (0.136)
<i>melanogaster</i> (South-East Asia)	♂♂	18	328–364 (346.3)	215–258 (233.5)	77.0–92.0 (82.8)	34.0–47.5 (43.3)	0.63–0.72 (0.67)	0.230–0.260 (0.240)	0.110–0.140 (0.128)
	♀♀	8	340–360 (347.0)	218–245 (233.9)	67.8–79.4 (76.2)	39.8–45.0 (42.6)	0.62–0.72 (0.67)	0.200–0.230 (0.220)	0.115–0.130 (0.123)
<i>novaehollandiae</i> (Australia)	♂♂	62	331–368 (349.6)	197–240 (217.0)	66.8–80.0 (74.9)	44.5–52.7 (48.0)	0.59–0.66 (0.62)	0.195–0.230 (0.215)	0.128–0.145 (0.137)
	♀♀	63	320–370 (346.9)	200–245 (220.3)	65.0–84.0 (75.6)	45.0–55.0 (48.8)	0.59–0.69 (0.63)	0.190–0.235 (0.218)	0.130–0.152 (0.139)
<i>papua</i> (New Guinea)	♂♂	3	347–353 (349.3)	224 (224.0)	67.6–75.2 (72.4)	45.6–49.4 (47.7)	0.64–0.65 (0.65)	0.194–0.214 (0.207)	0.131–0.142 (0.136)
	♀♀	12	334–360 (343.8)	218–234 (223.3)	73.6–86.0 (78.2)	41.7–50.4 (45.6)	0.62–0.68 (0.65)	0.217–0.239 (0.227)	0.125–0.142 (0.134)
<i>anhinga</i> (New World)	♂♂	10	347–368 (354.0)	246–270 (259.4)	85.0–96.0 (91.8)	39.5–44.0 (41.5)	0.71–0.75 (0.73)	0.248–0.270 (0.260)	0.114–0.122 (0.118)
	♀♀	8	327–354 (342.1)	238–269 (251.8)	75.5–88.5 (82.0)	37.5–44.0 (41.0)	0.68–0.77 (0.74)	0.230–0.253 (0.240)	0.112–0.125 (0.120)

plumages, short bills and tails, and relatively long, pale flesh-toned feet. Afro-Middle East and Oriental populations may be more alike in proportions and bare-part colours, attenuate cheek stripes and scapulars, and sexually similar breeding plumages, but differentiation is still marked. Both neck colour and throat patterns differ in breeding plumage, and the cheek stripe feathering in the Afro-Middle East group is shortly plumose, a state missing from both Oriental and Australasian groups. Upperwing patterns differ too, and from the Australasian group. In the latter, it is clearly two-banded and sexually dimorphic, the spotted grey shoulder band brighter in females than males. In the Oriental, it is sexually monomorphic yet even more brightly and contrastingly two-banded. But in the Afro-Middle East group, it is a dull in both sexes, the upperwing almost monotone with fuscous-copper shoulders except, to some extent, in the Middle East form.

Paedomorphism has played a significant role in differentiation, accounting for the paler head, neck and bare parts in non-breeding males and females of African and Oriental populations, creamy neck in all plumages in the Middle East, and grey-backed, white-ventered adult females in Australasia. Patterns on the upperwing and face and throat

in breeding plumage are of a different order, and may be implicated deeply in species recognition in sexual and social display. Focal elements in such behaviour are 'wing waving' and 'peering' with sideways head twisting on an outstretched neck (Cramp & Simmons 1977, Brown *et al.* 1982, Marchant & Higgins 1990). Both sets of movements have the effect of showing off the face and wing markings; and it follows that unfamiliar patterns there may hinder mating and serve as barriers to reproduction (*cf.* Price 2008: 273–297). Accordingly, we have given extra weight to divergence in nuptial face and upperwing pattern among the regional populations of Old World darters, leading us to separate Australasian, Oriental and Afro-Middle East groups as species. They are *novaehollandiae*, *melanogaster* and *rufa* respectively. Depths of mtDNA sequence divergence, as far as they go, are supportive (Kennedy *et al.* 2005). As sister species that represent one another in different geographical regions, these taxa form a superspecies separate from American *anhinga* (*pace* Dorst & Mougín 1979, Sibley & Monroe 1990). The latter is differentiated at deeper morphological levels also (Harrison 1978), a position corroborated by mtDNA data (Kennedy *et al.* 2005).

Within *rufa* and *novaehollandiae* there is further regional differentiation in morphology, but at a lower level. New Guinean *papua* resembles *novaehollandiae* in all plumage patterns, bare-part colours, size and proportions, but its females are consistently dark dusky-backed, in contrast to the mid to deep brownish grey tones in Australian females, and the pale shafts on the scapulars and rich grey centres to the wing-coverts are often reduced. Although such melanism may have been driven by a more humid environment (Gloger's ecogeographical rule), the difference is consistent and appears genetically entrenched; thus we agree with Rand (1938) in recognising *papua* subspecifically in the *novaehollandiae* complex. Within the *rufa* complex, Malagasy *vulsini*, though like African *rufa* in pattern and tone, has a browner head and rather washed-out cheek stripe with little blackish bordering, particularly in males, as well as paler, greyer, greater upperwing-coverts. Males also appear to be smaller than females (Table 3). Although these states may be affected by immaturity in the male sample screened (crimping on central rectrices is reduced), they are consistent across all parameters. Middle Eastern *chantrei*, which, as Kirwan *et al.* (2008) correctly point out, was referred in error to *A. melanogaster* by Sibley & Monroe (1990), appears to be part of the *rufa* complex too: it has the distinctive *rufa* pluming of the cheek stripe, and is *rufa*-like in size, proportions and sexual dimorphism, with ventral black from the lower neck down in both sexes. Its neck is nevertheless cream-toned in all plumages—even quite white in males, against which the black gular line above the cheek stripe stands out. The pale centres to the upperwing-coverts and scapulars are lighter, more silvery grey as well. Cramp & Simmons (1977) and Kirwan *et al.* (2008) included *chantrei* in *rufa* because of overlapping variation in foreneck and wing-coverts tone supposedly reported by Ticehurst, but we cannot confirm this observation nor, indeed, its reference. Accordingly, we treat *vulsini* and *chantrei* as subspecies of *rufa*. *A. r. chantrei* appears to survive today only in the Huweizah (Hawizhe) and Hoor-al-Azim wetlands within the lower Tigris-Euphrates basin in Iraq and Iran, although there is one recent record from northern Israel (Ottens 2006) where the species wintered regularly until 1957 (Shirihai 1996). Its decline and rarity needs recording on international registers of threatened fauna.

### Conspectus of Old World taxa of *Anhinga*

To conclude, we summarise the taxonomic findings of this study in the following sequential conspectus of the species and subspecies of Old World darters, together with a summary distribution of the taxa and suggested English names for the species. All species are considered to form a superspecies separate from *A. anhinga*, as indicated by the senior species-group name in square brackets.

***Anhinga [melanogaster] rufa* (Daudin, 1802)—African Darter**

*A. r. rufa*—sub-Saharan Africa

*A. r. vulsini* Bangs, 1918—Madagascar

*A. r. chantrei* (Oustalet, 1882)—lower Tigris-Euphrates wetlands (Iraq, Iran), formerly Lake Antioch = Amik Gölü (Turkey) before its draining, and northern Israel (in winter)

***Anhinga [melanogaster] melanogaster* Pennant, 1769—Oriental Darter**

Pakistan (Indus Valley), India, Sri Lanka, mainland South-East Asia (except Malay Peninsula), Greater Sundas, Philippines, Sulawesi, Sumbawa and ?Timor

***Anhinga [melanogaster] novaehollandiae* (Gould, 1847)—Australasian Darter**

*A. n. papua* Rand, 1938—lowland New Guinea and satellite islands

*A. n. novaehollandiae*—mainland Australia except central deserts; the subspecific identity of populations on Timor and Roti (Lesser Sundas, Banda Arc and Moluccas) remains to be established

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